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INTRASPECIFIC AGGRESSION AND POPULATION DISTRIBUTIONS OF THE SEA ANEMONE *METRIDIUM SENILE*

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Abstract

Aggregations of the sea anemone *Metridium senile* in Monterey Harbor sometimes contained only one clone (genetically identical individuals) but often contained two or more intermingled clones. The frequent occurrence of mixed clonal aggregations was perplexing, because *M. senile* uses fighting ("catch") tentacles in intraspecific agonistic interactions. A photographic survey of 19 quadrats showed that mixed clonal aggregations of anemones persisted throughout the 3.5 year study. Locomotion by the anemones, low frequency of nonclonemate contact, low population density, and infrequent occurrence of fighting tentacles were eliminated as possible explanations for the persistence of mixed clonal aggregations. Laboratory studies revealed differences among clones in the frequencies of fighting tentacle inflation and of injury to nonclonemates. We believe that low expression of these aggressive traits might permit intermingling of clones. However, high expression of aggressive traits was not found consistently in clones which were not intermingled, and therefore may not cause the segregation of such clones. Apparently, the most important factor contributing to the intermingling of clones was habituation of anemones to nonclonemate contact. The decrease in fighting tentacle inflation observed during two, six-day laboratory experiments was not due to fatigue, because contact with unfamiliar nonclonemates renewed aggression. We believe that habituation to nonclonemate contact occurs *in situ*, and that loss of habituation must occur occasionally to account for the occurrence of fighting tentacles.

Introduction

Detailed studies of the agonistic behaviors of sea anemones and certain other anthozoans may clarify the importance of competition for space in benthic marine environments. Recent research shows that some anthozoans demonstrate remarkable agonistic behaviors, including interactions among neighboring species of corals (Lang, 1973; Wellington, 1980), interactions between corals and anemones (Sebens, 1976), and elaborate intraspecific battles among genetically different individuals in several sea anemone species. Some anemones use acrorhagi in aggression (Abel, 1954; Bonnin, 1964; Francis, 1973a, b, 1976; Brace *et al.*, 1975; Bigger, 1976, 1980; Williams, 1978; Brace and Pavey, 1978; Ottaway, 1978; Brace, 1981), and some use "catch tentacles" in aggression (Williams, 1975, 1980; Purcell, 1977a). Many of these anemone species reproduce asexually, forming groups of genetically

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identical individuals (clones). Aggression, when it occurs, is between individuals of different clones or of different species, and is probably important in competition for space.

In addition to having feeding tentacles, some individuals of the sea anemone *Metridium senile* have a few special tentacles that can be inflated to a length of 4 to 5 times the diameter of the tentacle crown. These tentacles, called "Fangtentakeln" originally by Carlgren (1929), and more recently "catch tentacles" (*e.g.*, Hand, 1955), were long believed to be used in feeding. However, since recent work has shown that these tentacles are not used in feeding (Purcell, 1977a), but are used in aggression (Williams, 1975, 1980; Purcell, 1977a), they are referred to in the present paper as fighting tentacles. New contact of the tips of feeding tentacles with any anemone causes fighting tentacle inflation, but nematocyst discharge and resulting injury occur only when a fighting tentacle tip contacts a genetically different anemone (Purcell, 1977a).

On wharf pilings in Monterey Harbor, *Metridium senile* clones sometimes are separated from neighboring clones by an anemone-free zone, forming "segregated" clones. Individuals along the borders of such an anemone-free zone have fighting tentacles, and their aggressive behavior is thought to maintain the segregated distribution of the clones (Purcell, 1977a). More frequently, however, aggregations of two or more clones occur where individuals intermingle without an anemone-free zone, forming "mixed" clones. Often many individuals in these mixed clone aggregations bear fighting tentacles. We expected that mixed aggregations would not persist because aggressive interactions are known to occur among nonclonemates. The present study was undertaken to determine whether these mixed aggregations persist, and if so, to examine behavioral characteristics of different anemone clones that could promote the aggregations of more than one clone.

Materials and Methods

Observations of natural populations

The study area at Wharf No. 2, Monterey Bay, California, was in a well-circulated outer region of a port used for commercial fishing and pleasure boating. Haderlie and Donat (1978) have described the overall physical and biological environment at this wharf habitat. Anemone populations were on pilings that had been in place for about 50 years. In the present study, 19 perpetually submerged quadrat sites were selected with aggregations of *Metridium senile*. The sites measured 30 by 50 cm, and were chosen to represent a variety of clonal interactions among the anemones: three had anemones of only one identifiable clone, three had one clone with one nonclonemate anemone in its midst, four had roughly equal numbers of two or three mixed clones and few of these anemones had fighting tentacles, five had approximately equal numbers of two or three mixed clones and many of these anemones had fighting tentacles, and four sites had two segregated clones. Sites consisting of one predominant clone will be called "single clone"; sites with two or more clones intermingled will be called "mixed"; and sites with two clones separated from each other by an anemone-free zone will be called "segregated." Adjacent clones were distinguished by color, as described by Purcell (1977a), a characteristic which appears to be genetically determined, and is consistent within a clone (Hoffmann, 1976).

A numbered plastic tag nailed to the piling marked the bottom center of each site. Color transparencies were taken at each submerged site at six week intervals beginning in April, 1977. After five sampling periods, when such frequent sampling appeared superfluous, photographs were taken at twelve week intervals through April, 1978. Some of the quadrats were subsequently photographed at four to six month intervals through August, 1980.

Movements of anemones were monitored to test the extent to which the mixed clonal aggregations were labile. Individual anemones could often be identified between twelve week samples during the first year by their position relative to natural markers such as barnacles, and by their size, color, and possession of fighting tentacles. Small displacements were impossible to detect because orientation and expansion of the tentacle crowns varied. We used two hand-held slide viewers and a light table to optically superimpose and magnify two photographs taken of the same site on consecutive sampling dates.

Transparencies from the initial sampling were compared to those from a year later to determine changes in the percentage of anemones with fighting tentacles in each clone, and in the amount of nonclonemate contact. Transparencies were examined simultaneously as before, and at 7× magnification under a dissecting microscope to determine presence of fighting tentacles. Occasionally individual anemones were contracted such that the tentacles could not be seen, and therefore these individuals were not included in the analysis.

The percentage cover of anemones within an aggregation, including their tentacles, was used to assess the degree of crowding and tentacle contact. Percentage cover was quantified by viewing a color transparency of each study site with a dissecting microscope, and tabulating intercepts with anemones on a random array of points throughout the area of the slide (Kitting, 1980). Photographs taken of the sites after the first year of the study were examined using the same methods as before, but by then the original individual anemones could no longer be positively identified.

Laboratory observations of aggressive behavior

Anemones were collected from the pilings with a putty knife and kept isolated from other clones for 8 hours in flowing seawater. Undamaged anemones were then placed in plastic containers 10.5 cm square and 6 cm deep which had small holes near the top to permit water, but not anemones, to escape. Unfiltered sea water at 12–13°C flowed into a large plastic reservoir from which siphons supplied each container with approximately equal water flow. Anemones were fed larvae of brine shrimp, *Artemia salina.* The sediment and mucus accumulating in each container were vigorously rinsed away with sea water twice daily after each feeding. All anemones used in the experiments measured about 5 cm expanded column height.

Three sets of behavioral experiments were run. The first set used anemones from selected single and mixed clone quadrats at the end of one year of photographic sampling. These results were preliminary, and are used only to correlate field and laboratory results. The second and third sets of experiments, which did not use clones from monitored quadrats, tested clonal differences in aggression and tested habituation to nonclonemate contact. These anemones had five to eight fighting tentacles. Anemones were collected from five clones in mixed aggregations for both sets of experiments. Two anemones from each of two clones were placed in each container to form pairwise combinations of the different clones. Containers with clonemates provided information on aggressive activity without nonclonemate influence. Observations began 18 h after introduction of the anemones into the containers, when all anemones were attached and expanded. Anemones were observed during 0.5 to 1.5 h periods, totalling 11.5 h over 6 days, and 18 h over 5 days in the second and third sets of experiments, respectively. The clonemate and nonclonemate contacts of each anemone, the number of anemones with inflated fighting tentacles, and the number of fighting tentacles inflated per anemone were noted during each observation period. The injuries, visible as lumps of necrotic tissue, inflicted by fighting tentacles were also counted for each anemone daily.

If habituation to nonclonemate contact occurred, fighting tentacle inflations should decrease over time. However, such a decrease in aggression might also be explained by fatigue of the anemones due to experimental conditions. A test to determine whether the anemones were fatigued or habituated was conducted on the last day of both experiments. One hour of observations were made, then one anemone from a third clone (previously kept with clonemates in the laboratory) was placed in nonclonemate contact in each of several containers having pairs of other clones. Alternatively, an additional anemone from one of the two clones already present was introduced into each of several containers. Other containers remained unchanged for comparison. After the additional anemones had expanded, fighting tentacle inflations were monitored in all containers for 1 and 4 h in the second and third experiments, respectively.

Arcsine transformations used in calculations on percentages and statistical tests are from Sokal and Rohlf (1969).

Results

Observations on natural populations

Mixtures of two or more clones of *Metridium* were not expected to persist unchanged, because laboratory observations of their aggressive interactions showed that the anemones continually injure, and can kill, nonclonemates over periods of a few weeks (Purcell, 1977a). Seven hypotheses were formulated which could explain the occurrence of mixed clonal aggregations.

Hypothesis 1: *Anemones may change location such that nonclonemates avoid prolonged interaction.* Analysis of periodic photographs at 12-week intervals tested for such locomotion. During the first year, the mean percentage of anemones that changed locations noticeably was very low, 5.8% at all sites over the entire year. Movement in mixed sites tended to be slightly higher than in the other sites (Table I), but the difference was not significant (single classification analysis of variance (ANOVA)). A few anemones in segregated sites crossed the anemone-free zone and then remained in nonclonemate contact. In one segregated site, many individuals of one clone traversed the zone between clones, eliminating the anemone-free space. Anemones at all other experimental sites changed location very rarely. Hypothesis 1 was rejected as an adequate explanation for intermingled clones.

Hypothesis 2: *Anemones in mixed aggregations may not remain in tentacle contact with nonclonemates.* Tentacle tip contact has been documented as a stimulus for aggression in *M. senile* (Purcell, 1977a). The number of anemones in contact with nonclonemates was compared between the beginning of the study and after one year for every clone in mixed, single clone, and segregated sites in a two-way ANOVA. The numbers of nonclonemate contacts in the three types of sites were significantly different (Table I). As expected, mixed sites had much greater nonclonemate contact ($P < 0.001$). However, no significant change in the overall number of nonclonemate contacts occurred between two samples taken one year apart ($P > 0.10$). The percentage of anemones in mixed sites in nonclonemate contact was 92.9% at the beginning of the study, and was 96.5% at the end. Hypothesis 2 was rejected.

TABLE I

Characteristics of anemone populations at quadrats monitored photographically for one year.

	Type of anemone aggregation			Statistical probability
	Single clone	Mixed	Segregated	
Mean % of anemones changing location during one year	3.9 ± 4.8	9.6 ± 1.9	4.0 ± 1.4	$P > 0.25$ NS
Mean % of anemones in nonclonemate contact	0	92.9 ± 10.0	9.2 ± 3.5	$P < 0.001$
Mean % of anemones with fighting tentacles	5.5 ± 15.0	21.5 ± 16.6	57.8 ± 5.2	$P < 0.001$
Mean % cover of anemones	96.3 ± 0.8	93.7 ± 2.2	98.2 ± 1.9	$P > 0.10$ NS
Number of anemones	154	213	231	
Number of clones	6	25	8	

Except for the percentage of anemones changing location, percentages are based on measurements at the beginning of the study. See text for comparisons over the year. The values are means ± standard deviations. The probabilities expressed are from tests (ANOVA) using the actual numbers (not percentages) for each quadrat. The null hypothesis in each case was that no difference existed among the three types of sites.

Hypothesis 3: *Percentage cover of the anemones in mixed aggregations might be low, and thereby might minimize feeding tentacle contact, keeping aggression infrequent.* The mean percentage cover for all aggregations was very high, averaging 96.1%, with mixed sites having only slightly lower cover (Table I). A comparison of the percentage cover of anemones within aggregations of single clone, mixed, and segregated sites showed that the sites did not differ significantly (ANOVA, $P > 0.10$). Low percentage cover cannot explain persistence of the mixed clonal aggregations. Hypothesis 3 was rejected.

Hypothesis 4: *Anemones from clones in mixed aggregations may rarely form fighting tentacles.* The percentage of anemones with fighting tentacles was greatest in segregated sites (Table I). This is due to the quadrat placement which focused on the opposing borders of two clones where the fighting tentacles are found (Purcell, 1977a). For one clone, mixed, and segregated sites, the number of anemones with fighting tentacles was compared at the beginning of the study and after one year (two-way ANOVA). The number of anemones with fighting tentacles differed significantly among the three types of sites ($P < 0.001$). However, between the beginning and the end of the first year, no significant overall change occurred in the number of anemones with fighting tentacles ($P > 0.10$). The percentage of anemones with fighting tentacles increased over the year from 3.5 to 11.8% at single clone sites, from 21.5 to 23.8% at mixed sites, and from 57.8 to 58.9% at segregated sites. Hypothesis 4 was rejected.

The preceding measurements of *M. senile* populations at experimental sites all indicate that both mixed and unmixed populations changed surprisingly little over one year, and individual anemones often remained at the same attachment site and maintained nonclonemate contact for at least a year.

Eleven of the original quadrats with mixed clonal aggregations were photographed at intervals throughout 3.5 years. In all cases, quadrats contained the same anemone clones at the end of the study as at the beginning. Locomotion by the anemones, while undetectable over short time periods, produced noticeable changes in the arrangement of anemones over 3.5 years (Fig. 1). However, no segregation

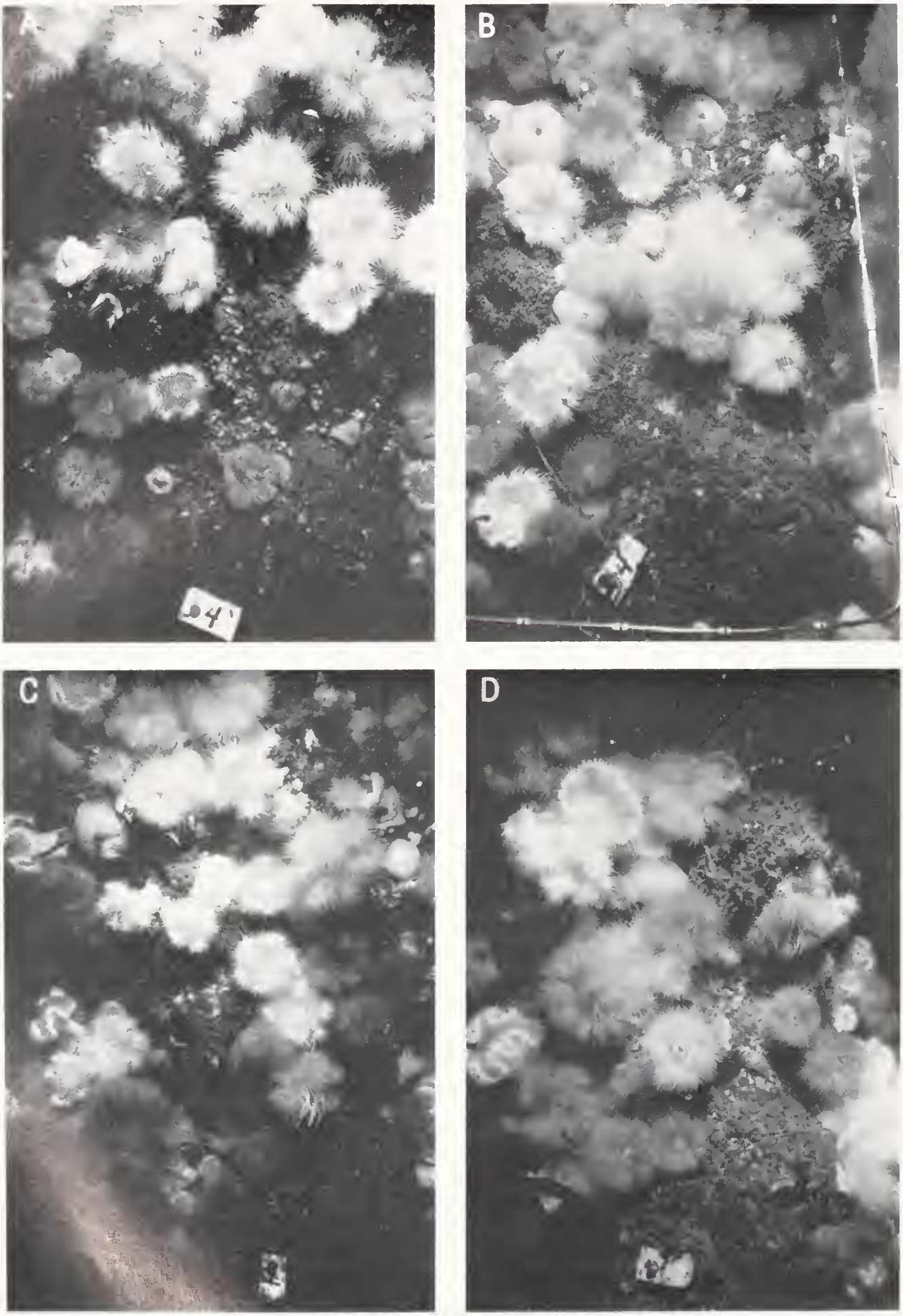

FIGURE 1. Photographs of one quadrat in a) May, 1977, b) April, 1978, c) January, 1980, and d) August, 1980. Anemones of three clones are intermingled; overall light gray, light gray with white banded tentacles, and orange (darker gray in the photograph) with banded tentacles. Fighting tentacles are the large, opaque tentacles near the mouths of some anemones. The scale markers in b) are 5 cm apart.

of the mixed clones occurred. Asexual reproduction and growth of the anemones, although not measured, undoubtedly contributed to the long-term changes in the photographed quadrats. These long-term observations upheld the conclusion from the detailed analysis over the first year, that mixed clonal aggregations persist with little change over time.

Laboratory studies of aggressive behavior

Hypothesis 5: *Clones may differ in the frequency of fighting tentacle inflation.* The numbers of inflated fighting tentacles were monitored in the laboratory, and related to population differences seen in clones from the photographed sites. In the field, the percentage of anemones with fighting tentacles in clones from mixed sites ranged from 0–100% (mean 21.5 ± s.d. 16.6%). In the laboratory, differences in behavior were obvious among the various clones; some clones had fighting tentacles inflated more frequently than did other clones (Fig. 2). However, anemones from clones having a high percentage of individuals with fighting tentacles did not necessarily inflate fighting tentacles frequently in the laboratory, nor was the reverse true (Fig. 2; $r = 0.32$, $P > 0.05$). One clone from a segregated site displayed one of the highest frequencies, even when in a container holding only clonemates. However, not all clones from segregated sites inflated fighting tentacles frequently, nor did all clones from mixed sites inflate them rarely (Fig. 2). This suggests that a higher frequency of fighting tentacle inflation in segregated clones was not sufficient to explain the anemone-free zone separating the two clones. Likewise, a low frequency of fighting tentacle inflation was not sufficient to explain the ability of clones to intermingle.

Anemones with fighting tentacles were taken from five different clones and used to test further for differences in aggressiveness among clones. The responses of each clone to the other clones paired with it in the laboratory, and the mean response

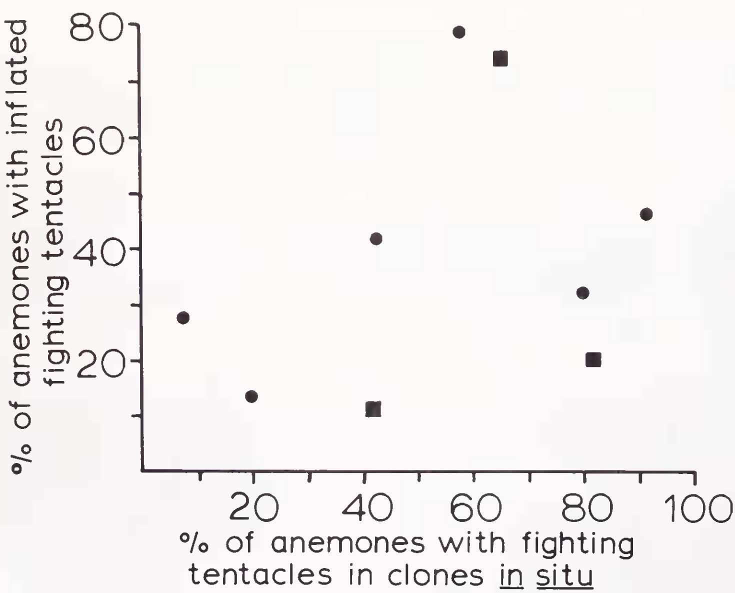

FIGURE 2. The percentage of anemones from different clones with fighting tentacles in their natural environment versus their inflation of fighting tentacles against nonclonemates in the laboratory. Squares = segregated clones, closed circles = mixed clones.

TABLE II

Comparison of fighting tentacle inflation among five anemone clones in experimental pairs.

"A" Clone	"B" Clone	Anemones in "A" Clone with fighting tentacles inflated: No.	Mean	No. of anemones in nonclonemate contact
1	2	11	9.50	13
	3	7		8
	4	14		18
	5	6		14
	1	1		
2	1	12	10.00	10
	5	8		11
	2	2		
3	1	6	3.75	7
	4	1		13
	5	4		16
	3	4		
4	1	4	2.33	18
	3	0		14
	5	3		15
5	1	5	5.50	15
	2	6		13
	3	9		17
	4	2		18

The numbers of anemones with fighting tentacles inflated were summed over 10.5 h of observation for each clone in each pair during the six day experiment.

for each clone, are given in Table II. A comparison of the number of these anemones with inflated fighting tentacles showed a significant difference among clones (ANOVA, $P < 0.025$). Clearly, the clones displayed different frequencies of fighting tentacle inflation. The responses of each clone might be expected to vary with the amount of nonclonemate contact experienced. However, the clones did not vary significantly in the number of anemones in nonclonemate contact during the experiment (ANOVA, $P > 0.25$). The differences among clones in the frequency of inflating fighting tentacles cannot be attributed to unequal nonclonemate contact. Hypothesis 5 was *not* rejected. Low frequencies of fighting tentacle inflation might contribute to intermingling of some clones.

Hypothesis 6: *Clones may differ in the infliction of injury upon nonclonemates.* Fighting tentacle adherence to a nonclonemate, with the resulting injury, causes the victim to inflate its fighting tentacles (Purcell, 1977a). This effect would be expected to escalate aggression in the experimental containers. The total number of fighting tentacles inflated over the six-day experiment were compared for each pair in the experimental clones (Fig. 3a). The number of fighting tentacles inflated was not significantly correlated between clones of a pair (Kendall Rank Correlation, $P > 0.05$). This is because the pairing of clones #1 and #4 differed substantially from the others. Both clones in each of the other pairs tended to show similar frequencies of fighting tentacle inflation, although (#1, #4) was an exception.

Injury might be a cause of enhanced aggression in nonclonemate interactions.

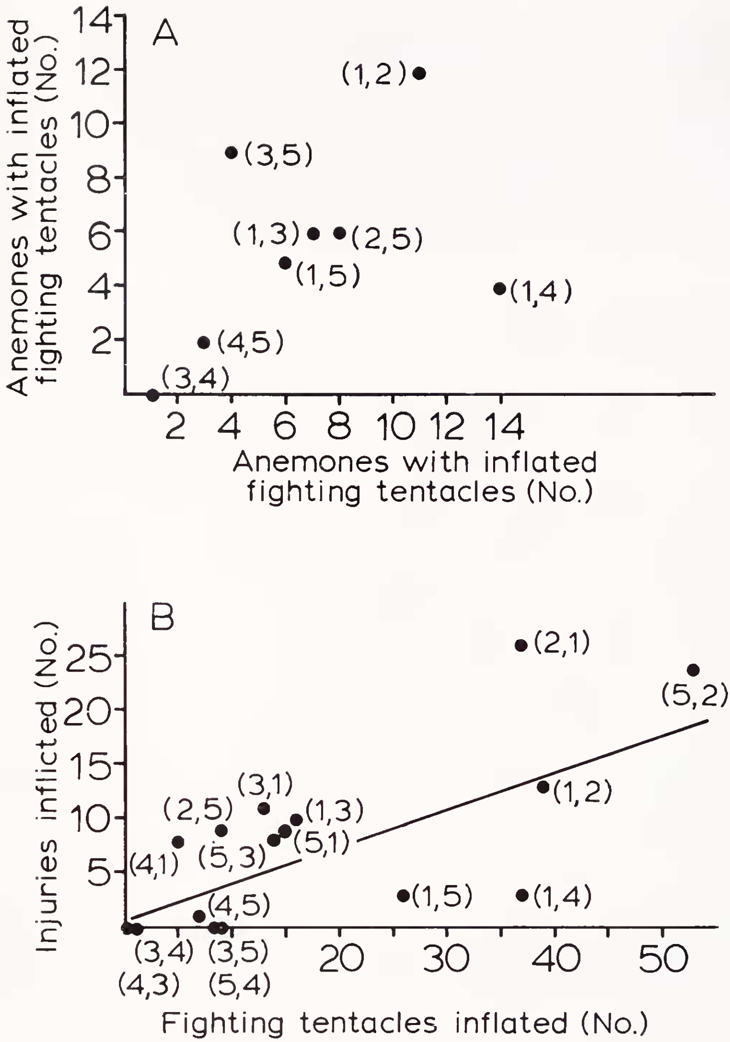

FIGURE 3. The effect of interaction between clones. Points are labeled with numbered clone pairs corresponding to the appropriate (x, y) coordinate numbers. Values represent totals for each clone during 11.5 h of observation. a) The number of anemones with fighting tentacles inflated tended to be similar for both clones in a pair with the exception of (1, 4). b) The number of fighting tentacles inflated by a clone was positively correlated with the injuries inflicted by that clone ($P < 0.005$).

The number of fighting tentacles inflated was significantly correlated with the number of injuries inflicted by each clone in each container (Fig. 3b, $P < 0.01$). Overall, more inflated fighting tentacles resulted in more injuries. However, in some clone pairs, fighting tentacle inflations were frequent, but injuries rare. In all clone pairs, fighting tentacles sometimes failed to adhere to nonclonemates even after prolonged contact of the fighting tentacle tip. Hypothesis 6 was *not* rejected. Infrequent injury to nonclonemates may contribute to the intermingling of some clones.

Hypothesis 7: *Anemones may habituate or adapt to nonclonemate contact.* The first set of behavioral observations showed a decline in fighting tentacle inflation over the course of the six day experiment. We use the term habituation to describe the observed decrease in response (fighting tentacle inflation) to a stimulus (nonclonemate contact). We have to assume that the quality of the stimulus is constant throughout the experiment. To test for habituation to nonclonemate contact, the number of anemones with inflated fighting tentacles per hour of observation was plotted for each day in two further sets of experiments (Fig. 4a). In one experiment, the number of anemones with inflated fighting tentacles per hour decreased from

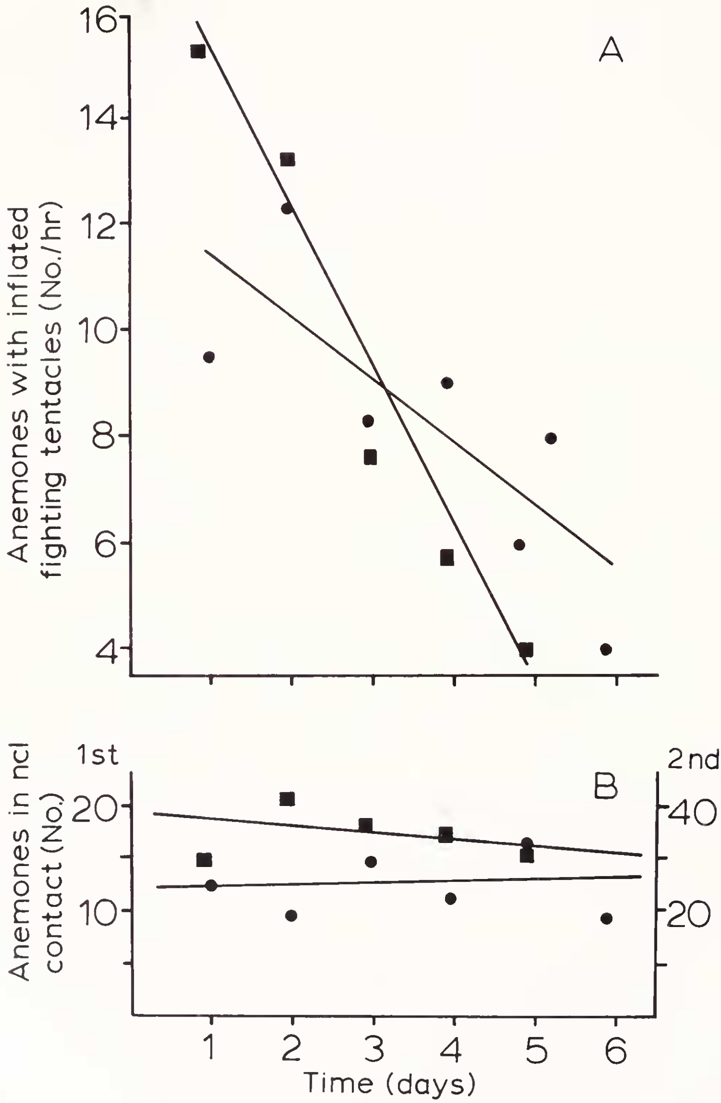

FIGURE 4. a) Decrease in aggression among nonclonemates confined together. Correlations for the two experiments: (●) r = −0.79, $P < 0.05$; (■) r = −0.96, $P < 0.01$. Each point equals the mean of 48 anemones. b) Frequency of anemones in nonclonemate contact during the same experiments. No significant change occurred over time.

peak activity of 12.3 anemones on the second day to 4.0 anemones on the sixth day. Similarly, the number of fighting tentacles inflated per hour decreased from 36 to 12. This strongly suggests a real decrease in aggression, although the decrease in the numbers of anemones fighting was not quite statistically significant (least squares regression, $P = 0.07$). The decrease in the number of anemones fighting in the next experiment was statistically significant (Fig. 4a, least squares regression, $P < 0.05$). At the same time, there was no significant decrease in the number of anemones in nonclonemate contact in either experiment (Fig. 4b), which eliminates reduced contacts as a cause of the reduced aggression.

To distinguish between fatigue and habituation as possible causes of the observed decrease in aggression, an anemone from a third clone was added to the established pairs of clones. If the observed decreases in aggression were due to fatigue, these new contacts should have resulted in continued low fighting tentacle activity. Instead, the mean number of inflated fighting tentacles increased dramatically in the containers which received a different nonclonemate (Table III). Within a few hours after contact with a new nonclonemate, much fighting tentacle activity occurred in anemones that had not inflated fighting tentacles for two or three days prior to the new contact. In containers to which no new anemones were added, the mean number of inflated fighting tentacles continued to decrease (Table III). Neither fatigue nor decreased nonclonemate contact accounted for the decreased fighting tentacle activity. These results indicate that the anemones habituated to nonclonemate contact. The addition of another anemone from one of the clones of an experimental pair caused some increase in aggression, but the sample size was too small to determine whether this was a significant effect (G-test, $P > 0.05$). It was not possible to determine from these results whether habituation was specific to the clones contacted. Hypothesis 7 was *not* rejected. Habituation appears to be a major factor contributing to intermingling of anemone clones.

Discussion

Several characteristics of the sea anemone *Metridium senile* were investigated in an attempt to explain: 1) how clones can be intermingled in spite of aggression which is known to occur between nonclonemates having fighting tentacles, and 2) how anemones of some clones are intermingled, while other clones are segregated.

Table III

Experiment showing that habituation, and not fatigue can explain the decrease in aggression observed over six days in two experiments.

	Fighting tentacles inflated (No./h)		
	Before	After	G-test
A No anemone added (16)	18	13	A *vs* B NS
B Anemone of same clone added (5)	4	8	B *vs* C NS
C Anemone of different clone added (8)	7	66	A *vs* C $P < 0.005$

Aggression was measured before and after additional anemones were placed in selected containers. If fatigue had occurred, aggression would not be expected to increase upon addition of any nonclonemate. Fighting tentacle inflations by the added anemones are not included. The numbers of replicate containers, each with four anemones, appear in parentheses.

Dense aggregations of two or more clones were stable over 3.5 years of observation; nonclonemates with fighting tentacles remained in contact at percentage cover equal to the cover within single clone aggregations. Low frequency of nonclonemate contact due to locomotion by the anemones, avoidance of contact, low percentage cover, and lack of fighting tentacles were eliminated as possible explanations for mixed aggregations of anemone clones.

Locomotion in natural populations of solitary actinians has been studied by Dunn (1977) in *Epiactis prolifera* and by Ottaway (1978) in *Actinia tenebrosa*. Ottaway (1978) states that following intraspecific aggression, the wounded anemone moved directly away from the site of wounding. We are aware of no previously published long-term population studies of aggregating actinians.

Clones were found to differ in several characteristics which would affect the intensity of nonclonemate aggression. Clones differed in the proportions of anemones with fighting tentacles and in the number of fighting tentacles per anemone. In the laboratory, clones differed in the frequencies of fighting tentacle inflation and in infliction of injury. These differences were not due to the amount of nonclonemate contact. Differences in aggression previously have been shown among clones of the anemone *Anthopleura krebsi* (Bigger, 1980), and among color morphs of *Actinia equina* (Brace *et al.*, 1975) and *Phymactis clematis* (Brace, 1981). A low expression of any of these characteristics could result in low levels of aggression in particular nonclonemate interactions. The intensity of aggression would depend upon the interaction of the clones involved.

Anemones from segregated clones did not display consistently high levels of the tested aggression traits that might make them particularly incompatible with other clones. These anemones seemed to habituate to nonclonemate contact, although the possibility that some clones might habituate less readily than other clones was not tested. It seems likely that segregated clones are a result of established, dense clones growing until they confront each other along a border, where nonclonemate interactions then cause fighting tentacles to develop (Purcell, 1977a) and an anemone-free zone to form. Mixing was observed between two previously segregated clones, hence segregation may be only temporary.

Aggression decreased between experimental pairs of *M. senile* clones kept together for 6 days in the laboratory. This may be the most critical factor in promoting mixed clonal aggregations of anemones. We use the term habituation to describe the observed decrease in fighting tentacle inflation. We do not intend to imply an understanding of the mechanisms involved, which conceivably could involve loss of the tendency to aggress (habituation, sensory adaptation), or loss of the stimulus to aggress (anemones becoming unrecognizable as nonclonemates). Habituation to mechanical stimuli has been experimentally established in *Hydra* (Rushforth, *et al.*, 1963) and in the sea anemones *Aiptasia* (Jennings, 1905) and *Metridium* (Allabach, 1905). Bonnin (1964) and Bigger (1980) found that the threshold for induction of the acroraghial response initially decreased, but then increased after repeated induction. These two examples suggest habituation, but fatigue was not eliminated as a possible explanation. Bigger (1980) cautions that not all specimens became totally refractory, and that thresholds remained low at induction intervals of 15 min or more. For *M. senile*, we show that contact by a nonclonemate elicited aggression in anemones habituated to another nonclonemate clone, thus showing that the anemones were not fatigued.

The persistence of mixed clonal aggregations of anemones and the fact that anemones habituate to nonclonemate contact are contrary to expectation, if intraspecific aggression is important in competition for space. Several intriguing questions are raised: (1) How important is intraspecific aggression in competition for space? (2) Since nonclonemates habituate, how are fighting tentacles maintained in the populations? (3) What advantage, if any, is conferred to the anemones by aggregating, even with nonclonemates?

In this 3.5 year study, there was very little apparent effect of intraspecific aggression on populations of *M. senile*. The Monterey wharf pilings appear to support far greater population densities of *M. senile* than do natural substrata (pers. obser.), and presumably would be subject to greater competition for space. However, fighting may be advantageous only if there is free space available. Intermixed nonclonemates in dense aggregations could continually battle each other with little to gain, unless one clone was able to kill off the other clones. Death as a result of fighting tentacle battles is not common in the laboratory, and apparently rare in nature. The importance of these battles may be greatest in causing the retreat of nonclonemates in areas where free space is available. Therefore nonclonemate habituation would ameliorate useless aggression where space is unavailable.

We believe that loss of habituation or adaptation to nonclonemate contact must occur in nature, because the anemones do have fighting tentacles and aggression does occur. *Metridium senile* exhibits periodic phases of contraction and extension which are related to light, feeding, and tidal cycles (Batham and Pantin, 1950; Robbins and Shick, 1980). Anemones in the field might contract periodically and therefore break contact with nonclonemates long enough to cause loss of habituation.

Francis (1973a) proposed several advantages of compact clonal organization for the intertidal anemone *Anthopleura elegantissima*. Some of these explanations could be modified to suggest advantages that might apply to aggregations of *M. senile*. Perhaps these anemones benefit more by aggregating, even with nonclonemates, than by keeping clones separated by aggressive interactions. The following possible benefits include: (1) minimizing or utilizing water motion—body size, shape, and behavior affect water flow patterns and drag forces exerted on benthic cnidaria (Wainwright and Koehl, 1976), and aggregating may reduce shearing forces of the water on individual anemones; (2) cooperative feeding—adjacent individuals of *M. senile* have been observed participating in the capture of food larger than single anemones could consume (Purcell, 1977b); (3) preventing larval settlement by potential space competitors—this could be effected by consumption of the larvae and by actual occupation of the available substratum; (4) reducing predation—the nudibranch *Aeolidia papillosa* is an important predator upon *Metridium* (Stenouwer, 1951; Waters, 1973; Harris, 1976). Aggregation of anemones may serve to reduce such predation by making a large part of the population less accessible to predators. Similar advantages for "colonial" growth of marine invertebrates were advanced by Jackson (1977), and these apply as well to aggregating anemones.

The arrangement of segregated clones of *Metridium senile* is like the clonal arrangement of *Anthopleura elegantissima*. Unlike *M. senile* clones, intermingling of *A. elegantissima* clones does not seem to occur (L. Francis, 1973a, and pers. comm.). Possible factors contributing to this difference in clonal arrangements of these two anemone species include the following: (1) *A. elegantissima* appears to remain in close clonemate contact after asexual reproduction (Francis, 1973a); and, (2) *A. elegantissima* may not habituate to nonclonemate contact (N. Withers, pers.

comm.). Because *A. elegantissima* clones remain discrete while *M. senile* clones often do not, it is tempting to speculate that evolutionarily, intraspecific competition for space may have been more important in *A. elegantissima* habitats.

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